The regulatory formation of mechanical tissue.[1]

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The prevalent notion of the influences which affect the progress on growth is doubtless that which one finds in the manuals on plant physiology most in use at the present day. In these manuals growth is set forth as governed largely by mechanical forces; by increase and decrease of pressure, and this pressure not acting as a stimulus but as a mechanical force. In Sachs' "Lehrbuch" of 1874 and again in his "Vorlesungen" of 1882 is a detailed elaboration of his mechanical theory; Vines' "Physiology of Plants" (1886) follows Sachs closely; while Pfeffer's "Physiologie" (1881) shows a little breaking away from the theory of Sachs, in that he gives contact as a stimulus to the formation of tissue, a phenomenon therefore of irritability.

It may not be devoid of interest to review briefly the steps by which this mechanical theory of growth gained its hold in the minds of botanists.

As the result of his well-known experiments, described in 1803, Knight[2] expressed the belief that the cortex of trees by its pressure exerted a restraining influence on growth in diameter, and that any means which reduced this pressure, such as the swaying by the wind, would allow a greater flow of nutritive fluid to the place and hence promote growth.

In 1859, Hofmeister[3] established the fact of interacting tissue tensions in a longitudal direction in growing plant organs.

Kraus,[4] in 1867, followed up the work of Hofmeister and discovered transverse tissue tension. Among his conclusions is this: that the curvatures due to geotropism, heliotropism, shaking by storms, and so forth, are accompanied by an excessive growth on the convex side, this excentricity of growth

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[1]Read before Section G of the A. A. A. S. at the Brooklyn meeting, August 1894.

[2]Knight, Philos. Trans. Roy. Soc. Lond. —: 280–3. 1803.

[3]Hofmeister, Ueber die Beugung saftreicher Pflanzentheile durch Erschütterung. Ber. d. k. sächs. Gesell. d. Wiss. —: 194. 1859.

[4]Kraus, Die Gewebespannung des Stammes und ihre Folgen. Bot. Zeit. **25**: 105. 1867.

being caused by the flow thitherward of nutritive fluid, made possible by the reduction of tension on the convex side.

It will readily be seen that while Knight assumed tension of tissues to be a controlling factor in the growth in diameter of trees, Kraus extended this causal relation to all kinds of increase of tissue. It remained now for that master-builder, Sachs, in the first edition of his Lehrbuch, in 1868, out of the material furnished by his pupil Kraus, by Hofmeister, and by Knight, to construct the framework of a mechanical theory of growth, which he subsequently elaborated in his later manuals, after the researches of de Vries and Detlefsen.

De Vries,[5] in the period from 1872 to 1876, had experimented in increasing and decreasing the pressure of the cortex of trees by winding about stems ligatures of twine in the first case, and by making longitudinal slits in the cortex in the second case. With his ligatures he obtained, so he believed, autumn xylem in the spring time; and by slitting he claimed to produce spring xylem in the autumn. His conclusion is obvious: cortical pressure must be the cause of the formation of annual rings.

Detlefsen,[6] another pupil of Sachs, published in 1881 his observations and deductions on excentric growth, and starting with the premises that all expansion of cells is due to the hydrostatic pressure of the cell-contents and that any external resistance to this internal pressure would diminish the effectiveness of the hydrostatic pressure, he drew the conclusion that the amount of growth was determined solely by the differences between these two forces. Thus he accounted for all excentricities of growth in stems and roots of woody plants according to the increase or decrease of the cortical pressure. Thus branches of trees that extend horizontally should show the more tissue below; and curving branches should show the greatest formation of tissue on the concave side, since during secondary growth a longitudinally concave cortex has its tension reduced, but a longitudinally convex increased.

Bringing together in small space the chief observations on

[5]De Vries, Flora —: 241. 1872; —: 97. 1875: —: 2. 1876.–De l'influence de la pression du liber sur la structure des couches ligneuses annuelles. Extrait d. Archives Neerlandaises **11**: —. 1876.

[6]Detlefsen, Versuch einer mechanischen Erklärung des excentrischen Dickenwachsthum verholzter Achsen und Wurzeln. Arbeit. d. bot. Inst. in Würzburg **2**: 670–87.

which Sachs and his school built their theory, we have the following eight statements, the truth of the last two of which is not without exceptions:

1. Between all growing tissues both longitudinal and transverse tensions are present, the outermost tissues seeking to contract while the innermost are seeking to expand.
2. Swaying of a plant promotes growth from the cambium.
3. Ligatures about woody stems decrease the number and size of the xylem elements.
4. Slitting the cortex longitudinally promotes growth from the cambium.
5. Abrading the dead part of bark promotes growth from the cambium (Knight[7]).
6. Normal clefts in the bark of trees deepen in the early spring.
7. Branches and roots of trees show excentricity of growth and the greatest growth is on the lower side, or when flexed on the concave side.
8. In the curving of stems due to geotropism, heliotropism, etc., the greatest growth in thickness is on the convex side.

Granting for the moment that all of the foregoing statements are facts, it is rather surprising that the mechanical theory of growth could have gained such general credence when two of its vital supports were pure assumptions. In the first place it was necessary to assume that extension of cells is but the stretching of hydrostatic pressure from turgidity; and in the second place, that the resistance offered by the cortex is great enough to control the amount and direction of cambium growth.

In 1884 Krabbe published a research which showed the incorrectness of the second assumption, and last year Pfeffer showed the untenableness of the first.

Krabbe[8] measured the compressing force of the cortex of many trees finding it to be always less than one atmosphere. Its increase of pressure from spring to autumn is never more than a fraction of one atmosphere while in many trees the increase is hardly to be measured.

By using a ligature with graduated weight this botanist

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[7] Knight l. c.

[8] Krabbe, Ueber das Wachsthum des Verdickungsringes und der jungen Holzzellen. Abhl. d. k. Akad. d. Wissensch. Berlin. 1884.

found that to check the growth of the cambium or to alter the size of cells required a pressure of three to five atmospheres, and from twelve to fifteen atmospheres to stop all growth. The pressure of the cortex must be, he concluded, from three to five times what it actually is to influence growth.

Thus the pressure of the cortex of woody trees is shown to exert little or no influence on the growth of the cambium; and this assumed support for the mechanical theory falls. With it also falls the time honored explanation of the cause of annual rings.

That the first assumption in support of the mechanical theory of growth—that extension is mere stretching—does not rest upon fact was demonstrated by Pfeffer.[9]

This author by an ingenious method was able to determine that cell membranes will extend till they feel no internal stretching force. Now if extension were the result of stretching alone, this condition could not be brought about, for the membrane would then be always in a state of tension.

If now growth is not controlled in a merely mechanical way by the pressure of tissue, we must look for some other explanation. Without attempting a discussion of the broad subject of growth, it has been and can be shown that growth especially of mechanical tissues is very often the result of self-regulation. It is true that the last statement does not propose the real cause; it is a confession of ignorance. But it removes the growth referred to from a mechanical phenomenon to one of irritability. This is the argument which I am making.

Let us now in the light of what has last been said examine some of the phenomena on which the founders of the mechanical theory based their argument, not forgetting however that the falsity of the theory has already been shown.

De Vries' experiments in placing ligatures about branches of trees gave the effect of unnatural pressure, not at all comparable with normal cortical pressure, and produced in the spring time, not autumn wood, as he said, but a deformed growth with smaller cells than in normal spring wood and with thinner walls than in normal autumn wood. There can be no doubt of the truth of this statement, for all of Krabbe's

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[9]Pfeffer, Druck- und Arbeitsleistung. Abhandl. d. k. sächs. Gesells. d. Wiss. **20**: —. 1893.

results in similar experiments on trees as well as mine on several herbaceous and shrubby plants point to the same conclusion. Knight's result on removing the outer dead part of the bark and de Vries' on making longitudinal slits in the cortex of trees should be referred to irritability and border closely upon regulatory action. Krabbe showed conclusively that the xylem formed subsequently to slitting in the autumn is not spring wood as de Vries thought. It is a response made to the injury of the knife.

The excentricity of branches and roots considered by Kraus and made much of by Detlefsen does not conform to the rules laid down by these two authors. I have found that the strongest development of tissue is often present on the convex side, but often also on the concave side. *Gladiolus communis* is an example of a plant forming an excess of tissue on the convex side of a geotropic curvature of the stalk, while *Ailanthus glandulosus* Desf. furnishes an example of excessive growth on the concave side. Detlefsen stated that horizontal branches have the greatest development on the lower side. In the Quince (*Pirus cydonia*) I have found it greatest on the upper side. Moreover a branch that in part of its extent is convex upward, and, farther out, convex in the opposite direction, does not change its excentricity with the change of curvature. If this statement does not hold true for all plants, it does for many, as my own observations have convinced me. According to Detlefsen's rules, the buttresses which extend on the trunk of a tree from the base of the branches downward and from the roots upward ought to reverse their position.

If we refer these variations to phenomena of regulation, we have a theory that is tenable; for one plant may regulate in one way and another in another way.

The formation of a larger amount of mechanical tissue under the stimulus of swaying agrees well with the notion of regulatory formation. What better illustration could be desired? What greater need of strengthening itself could a plant feel?

Another case of regulatory growth is furnished by the behavior of climbing organs as determined by Darwin[10] and by Treub.[11] Cause such an organ to grow free from contact

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[10] Darwin, Climbing Plants 48, 50, 51. 1876.
[11] Treub, Ann. du Jard. Bot. de Buitenzorg **2:** —. 1882.

and it remains weak. Mere contact with a solid body, however, calls forth a great development of strengthening tissue, which increases still more when the organ begins to feel the weight of the stem which it supports. The first strengthening tissue is here laid down as a response to contact; its increase is the regulatory response of the plant to the strain which it feels. Increase artificially the strain on the suspending organ and by regulation it will increase enormously its mechanical tissue, as I have had an opportunity to observe by examining the material prepared by Herr von Derschau, the description of which is soon to be published.

Similar results were obtained by Hegler[12] when he subjected stems and petioles to a pulling force. The petioles of a certain plant, for instance, in their normal condition, broke when subjected to a pull of 700^g; they were given for five days a pull of 500^g, and then broke at $1,600^g$; others, pulled for five days by 500^g, were then pulled by weights of $1,200^g$ for five days longer, and then broke at a strain of $6,500^g$. In ten days these petioles had increased their tensile strength five-fold. The strengthening was brought about in some plants by the development of collenchyma or sclerenchyma in the cortex, in others by the increase of the hard bast, in others by a greater growth of xylem, and still in others by a combination of two or more of these methods.

Corresponding results to those of Hegler I have recently obtained in the roots of young plants of *Helianthus annuus* and *Cucurbita pepo*, by attaching to the plants weights suspended over pulleys. In these experiments not only was the tissue strengthened, but the roots grew with a larger diameter than normally.

Thus far the attempt has been made to show that when an unusually heavy stress has been laid upon the plant, the plant responds by increasing the mechanical tissue. But if the plant be a self-regulatory organism, it might be expected that when the normal stress is reduced, the plant would form less than the normal amount of mechanical tissue. And the surmise has been proven to accord with the fact, first by the experiments of Knight ninety years ago, when he prevented the swaying of young trees in the wind by fastening them to

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[12]Pfeffer reported these experiments as, R. Hegler's Untersuchungen über Einfluss von Zugkraft. Ber d. k. sächs. Geselsch. d. Wissensch. December, 1891.

stakes, and secondly, by the results which I have obtained by enclosing internodes of stems in plaster casts.

A general result in all my experiments, performed on scores of plants, embracing twenty-five species and a dozen genera, is the lack of the development of the mechanical tissue. The casts employed were from 3^{cm} to 5^{cm} in length, and thus a segment of the stem was freed from the most of the strain to which it would normally be subjected. There could be no lateral swaying, nor could the confined segment feel the full weight of the stem above. It is, of course, true that with an envelope of plaster, growth must soon be brought to a standstill by mechanical means, and therefore that less than the normal amount of supporting tissue could be formed. But that the lack of formation of mechanical tissue within the enclosed segments was not due merely to mechanical causes will appear from the two following reasons: In the first place, the young cells of the pith, of the collenchyma in the cortex, of the hard bast, and of the xylem that were formed before the casts were applied, did not, well within the casts, reach their normal thickness of wall. In the second place, corresponding tissues within but near the limits of the casts became thicker-walled than normally. Thus we have, at two places within the same cast, tissues in the one case, where there is little or no external stress, remaining abnormally thin-walled, but in the other case, where there is great stress, becoming abnormally thick-walled. This abnormal increase in the thickness of membranes in the region of the limits of cast is worthy of more than passing notice. It must be at the limits of the plaster envelopes that these plants felt the greatest strains from lateral swaying by the wind and from supporting the stem, as the breaking of several of them by the wind demonstrated. The thickening of membranes was always greatest just at the surface of the casts, and from that level it decreased both upward and downward, extending into the cast for a distance of a centimeter. The contrast was very striking; within the distance of a centimeter one could pass from a cross-section composed wholly of thin walls to one composed mostly of unusually thick-walled elements. All kinds of tissue took part in this great development, but especially the pith and cortex, since the production of new cells from the cambium was mostly prevented by the mechanical conditions. I see no way of explaining the results of these

experiments except as regulatory phenomena. Try the different hypotheses of pressure, tension of tissues, relation between size of cells and thickness of membrane, and so forth, and none of them is satisfactory.

There is no claim made here that all growth of mechanical tissue is regulated by stress. It is influenced probably by transpiration, as the researches of Kohl[12] seem to indicate, and there is doubtless also an hereditary factor.

There is yet one feature to be added to the subject of regulatory growth. In my experiments, *Vicia faba* and *Melianthus majòr*, after growing in casts for several weeks, were released, and then showed a great constriction at the place where the growth had been confined. Within three or four weeks this constriction had entirely disappeared. Microscopical examination showed that, since the removal of the cast, there had been in all the plants an excessive development from the cambium, in the place of constriction, reaching in one case 40 per cent. to 50 per cent. more xylem elements in the abnormal segment than in the normal parts, above and below it. On the removal of the casts the weak segments felt suddenly the full weight of the stem. They responded by building a sufficiency of supporting tissue. There is reason, too, why there should have been more than the normal amount formed. The plaster was laid about these stems while the pith was still expanding, and the vascular zone moving outward from the center. The cast checked this movement, and by subsequent development within the rigid envelope, the supporting xylem cylinder was fixed nearer the center than normally. When released from the confinement, a greater radial thickness of mechanical tissue was needed in the narrower cylinder than in the normal cylinder to give the same degree of strength.

By the expression "regulatory growth," we do not come to the actual means or to the specific stimulus for that growth. We may say that the plant has the ability to respond to stress, but the notion *stress* is complex, and will doubtless by future research be subdivided. But this much seems certain: The formation of such growths as have been recounted in this paper is no longer to be explained as simple mechanics, but rather as a member of the increasing number of phenomena of irritability.

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[12]Kohl, Die Transpiration der Pflanzen. Braunschweig. 1884.